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PRIMARY RESEARCH PAPER

Spatial and temporal variation in phytoplankton community structure in a southeastern U.S. reservoir determined by HPLC and light microscopy

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Abstract Spatial and temporal variation in phytoplankton community structure within a large flood-control reservoir (Sardis Reservoir, MS, USA) was investigated in relation to variation in physicochemical properties, location within the reservoir, hydraulic residence time (HRT), nutrient concentrations, temperature, and light conditions over a 14-month period. During periods of short HRT, phytoplankton communities throughout the reservoir were homogeneous in biomass, composition, and production. With a gradual increase in HRT from spring to summer, spatially heterogeneous phytoplankton communities developed along the longitudinal axis of the reservoir. During this period of longer HRT, diatoms and chlorophytes were a larger proportion of total phytoplankton biomass at shallow and more turbid locations near the head of the reservoir, whereas cyanobacteria were a larger proportion of the community at deeper and less turbid locations closer to the outflow. Seasonal succession of the phytoplankton community was represented by high abundance of diatoms in spring, increasing biomass of cyanobacteria through summer, and a secondary bloom of diatoms in fall. Species of *Cyclotella*, *Asterionella*, *Nitzschia*, and *Ankistrodesmus* were among the first colonizers in the early growing season, closely followed by *Aulacoseira*, whereas species of *Staurastrum* and *Tetraedron* appeared later in the spring. Species of *Synedra*, *Crucigenia*, *Selenastrum*, *Scenedesmus*, and *Merismopedia* occurred throughout the sampling period. As the diatoms started to decrease during mid-spring, cryptophytes increased, prior to dominance of species of *Pseudanabaena* in summer. Reservoir management of HRT, in combination with spatial variation in reservoir morphology and seasonal variation in temperature and riverine nutrient inputs, creates seasonally variable yet distinct spatial patterns in phytoplankton community biomass, composition, and production.

Keywords Phytoplankton · Plankton · Reservoir · Lakes · HPLC

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Introduction

Reservoirs combine features of rivers and lakes and, in fact, have been described as "river-lake hybrids"

(Kimmel et al., 1990). The degree to which a reservoir resembles a river or a lake depends on how and for what purpose the reservoir is managed, the time of year, reservoir morphology, and location within the reservoir. Reservoirs managed for drinking water supply or for hydroelectric power, where water inputs and removal are in balance, may vary little on a seasonal basis in surface area, volume, depth, and hydraulic residence time (HRT), while still experiencing horizontal advective transport (Ford, 1990). In contrast, reservoirs managed for flood-control can vary dramatically on a seasonal basis in rates of water removal, surface area, volume, depth, and HRT. Such reservoirs are more like rivers at times of the year when water is rapidly being withdrawn, but become more hydrologically stable and lake-like at times of the year when the reservoir is filled (Ochs & Rhew, 1997).

At times of the year when HRT is at a maximum, reservoirs typically develop a longitudinal gradient in riverine to lacustrine conditions, and an associated gradient in physical and chemical properties (Kimmel et al., 1990). In general, as one moves from the more riverine upper to the more lacustrine lower portion of a reservoir, it becomes deeper and broader, and the water becomes more clear and nutrient depleted due to reduction in current, development of thermal stratification, and sinking of suspended sediments (Bettoli et al., 1985; Ramberg, 1987; Soballe & Kimmel, 1987; Bailey-Watts et al., 1990; Kimmel et al., 1990; Zohary et al., 1996). Adding to reservoir spatial complexity, along the length of the reservoir, tributaries of differing water quality can lead to localized conditions distinct from the main channel, and further contribute to spatial heterogeneity (Kimmel et al., 1990).

Where there is a gradient in physicochemical conditions, a gradient in phytoplankton community characteristics can be expected. For example, during summer, with a decline in nutrient availability from the more turbulent, riverine to more stratified, lacustrine regions of a reservoir, there is commonly a decline in phytoplankton biomass and biomass production (McCullough, 1978; Knowlton & Jones, 1995; Ochs & Rhew, 1997; Schallenberg & Burns, 1997; Buckaveckas & Crain, 2002).

Compared to natural lakes, there has been much less research investigating the extent to which a reservoir phytoplankton community varies, either spatially or with time, in taxonomic composition (Nogueira, 2000). The purpose of this study was to determine the degree of spatial, as well as seasonal variation in phytoplankton taxonomic composition, biomass, and productivity within a large flood-control reservoir, Sardis Reservoir, Mississippi. We hypothesized that spatial variation in phytoplankton community composition occurs when there is a gradient in riverine to lacustrine conditions and in the associated physicochemical conditions within a reservoir. Samples were taken over the course of 14 months at six spatially distributed stations along the longitudinal axis and major tributary embayment areas of Sardis Reservoir. Phytoplankton community characteristics were examined in relation to seasonal and spatial variation in nutrient availability, temperature, light conditions, and hydraulic retention time. The patterns we detected in phytoplankton community properties may be applicable to other flood-control reservoirs in the United States, as most reservoirs are located at similar latitudes, between 33°N and 42°N, where large natural lakes are uncommon (Kalff, 2002).

Methods

Study site

Sardis Reservoir was constructed after the great Mississippi River flood of 1927 with the purpose of controlling local flooding and movement of water into the Mississippi River. It was constructed in 1940 by damming the Little Tallahatchie River which drains the Little Tallahatchie watershed (LTW), an area of about 3,900 km^2. (Fig. 1).

The LTW consists of about 45% forest, 34% cropland or pasture, 11% urban/residential or miscellaneous uses, and 10% open water/reservoir (USDA-NRCS, 2007). There are three major sub-watersheds drained by creeks entering Sardis Reservoir from the southeast. The Clear Creek sub-watershed is 122 km^2. in area and consists of 60% forest, 25% agriculture, 3% urban/residential, and 12% open water. The Toby Tubby sub-watershed is 150 km^2. in area and consists of 45% forest, 10% agriculture, 35% urban/residential, and 10% open water. The Hurricane Creek sub-watershed is 85 km^2. in area and consists of 50% forest, 36% agriculture, 8% urban/residential, and 6% open water (unpublished aerial photos taken in 2005,

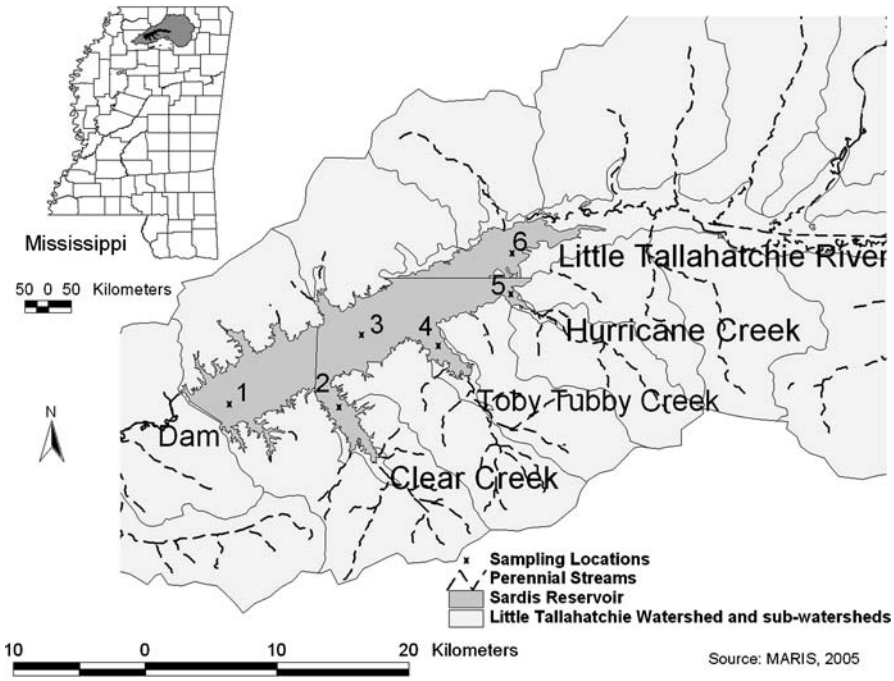

Fig. 1 Sardis Reservoir in the Little Tallahatchie watershed, northeastern Mississippi. The lake area illustrates the conservation pool water level (71.9 m above mean sea level). Numbers in the map indicate six sampling locations**:** Station 1: Down-lake; Station 2: Clear Creek embayment; Station 3: Mid-lake; Station 4: Toby Tubby Creek embayment; Station 5: Hurricane Creek embayment; Station 6: Up-lake

personal communication with H. Patterson, USDA, Oxford, MS).

Flood control operation and seasonally variable amounts of runoff from tributary streams result in large seasonal changes in water level and flow rates (Aumen et al., 1992). By releasing water in late summer and through the winter, the reservoir is drawn down to a minimum surface area of <50 km^2 in preparation for the annual rise of the Mississippi River with northern snow melt and rain during spring. Starting in mid-spring, water release is minimized and the reservoir is allowed to fill to its maximum surface area of over 120 km^2. (Ochs & Rhew, 1997).

Sampling

The reservoir was sampled from March 2004 to April 2005. There were a total of 15 sampling dates, with one to two site visits per month. Samples were not taken between December and February, when water retention time is short (<100 days), and spatial variation in phytoplankton community properties was not detected previously (Ochs & Rhew, 1997). Samples were collected at three stations (stations 1, 3, 6) along the longitudinal axis of the reservoir and three stations (stations 2, 4, 5) within major tributary (Clear Creek, Toby Tubby Creek, and Hurricane Creek) embayments (Fig. 1). Station 1 is the down-lake region, nearest to the dam and outflow, station 6 is the up-lake region, near the mouth of the river, and station 3 is the mid-lake region, at the middle of the reservoir. Samples were not collected at station 5 in September–November, 2004 as it was too shallow and thus inaccessible from the reservoir.

At all stations, water samples were collected at 0.5-m depth in the mixed layer as three replicates in 2-l HDPE Nalgene bottles. Although depths of mixing varied between sampling locations (see "Results"), the 0.5-m depth was considered representative of the mixed layer for each sampling site. Samples were kept cool and dark until processing, within 2–4 h after collection.

Physical and chemical properties

Temperature and oxygen profiles were measured in the field using an YSI Model 57 oxygen meter. Light extinction profiles were obtained using a Licor LI-1000 radiometer with a spherical quantum sensor and deck-mounted reference cell. Water transparency was measured as turbidity in the laboratory with a Hach Model 2100A turbidimeter. Mixing depth was estimated by profiles of oxygen and temperature.

Total dissolved nitrogen (TDN) and total dissolved phosphorus (TDP) were measured with an Astoria auto-analyzer in water filtered through Whatman GF/F filters. The filtrates were digested with alkaline persulfate prior to analysis (Charles & Kryskalla, 2003).

Hydraulic water residence time, in days, of the reservoir was calculated by dividing daily measurements of volume (in km^3) by daily measurements of discharge (in km^3 day^{-1}). Lake volume was obtained from a hypsographic curve for Sardis Reservoir. Lake elevation and discharge measurements are made daily at the dam by the U.S. Army Corps of Engineers, Vicksburg District (USACE, 2005).

The saturating intensity of light for phytoplankton photosynthesis in Sardis Reservoir was experimentally determined, using photosynthesis-irradiance curves, as about 400 µmol PAR m^{-2} s^{-1} (data not shown). The depth to which this saturating light level occurs was determined for stations 1 and 6 from light extinction coefficients determined on all sampling dates. For these calculations, we used 1,200 µmol PAR m^{-2} s^{-1} (I_o in the equation for light extinction, Kalff, 2002) as the maximum light intensity entering the water on a typical sunny day.

Phytoplankton primary production

Light-saturated volumetric primary production was measured in the laboratory for all sites at all dates by the fixation rate of radio-labeled carbon dioxide. About 24 ml of water samples were inoculated with 25 µl of $NaH^{14}CO_3$ (20 µCi ml^{-1}) in closed glass serum vials and incubated for 2–3 h at in situ temperature and 550–560 µmol PAR m^{-2} s^{-1} irradiance. Following incubation, the samples were filtered through GN-6 0.45-µm Metricel membrane filters. The filters were placed in 7-ml scintillation vials and acidified with 0.1 ml of 1N HCl to remove unincorporated dissolved inorganic carbon (DIC). After 24 h, ethyl glycol monoethyl ether was added to dissolve the filters, a few hours after which scintillation fluid was added and radioactivity measured in a Beckman scintillation counter. Total DIC assimilated per time was calculated from the ratio of radio-labeled carbon assimilated to available DIC (Ochs & Rhew, 1997; Wetzel & Likens, 2000).

Phytoplankton biomass and composition by pigment analysis

High performance liquid chromatography (HPLC) was used to identify the presence and relative importance of major taxonomic groups of phytoplankton from their diagnostic pigments (Jeffrey et al., 1997; Pickney et al., 2001; Pearl et al., 2003). We measured chlorophyll *a* (Chl *a*) biomass and five division-level pigments [chlorophyll *b* (Chl *b*), fucoxanthin, zeaxanthin, peridinin, and alloxanthin]. Chl *b* was used as a diagnostic pigment for estimation of chlorophyte biomass, fucoxanthin for bacillariophyte (diatom) biomass, zeaxanthin for cyanobacterial biomass, peridinin for dinoflagellate biomass, and alloxanthin for cryptophyte biomass (Jeffrey et al., 1997). Although zeaxanthin does occur at low concentrations in some chlorophytes, the proportion of zeaxanthin to Chl *a* is higher in cyanobacteria (Schlüter et al., 2006). Although Chl *b* is also a major pigment in euglenoids, they were not abundant in this reservoir.

Phytoplankton pigment extraction and determination were conducted using a slight modification of the method of Jeffrey et al. (1997). Water samples (200–400 ml) were filtered through Whatman GF/F filters under low vacuum pressure (<380 mm Hg), and filters stored in an ultra-cold freezer (−70°C) until pigment extraction. For extraction, filters were cut into small pieces and soaked in 90% acetone for 2 h at 4°C. The filter-acetone mixture was sonicated under low light and in an ice-bath for 30–60 s using a Fisher Sonic 60 Dismembrator. The filter residue with acetone was centrifuged at 2,000 rpm for 2 min, and the supernatant filtered through a 0.4-µm Millex PTFE filter prior to pigment separation by HPLC.

The HPLC system consisted of a photodiode array detector (Dionex PDA 100), pump (Dionex P580), and reversed-phase silica based column (Alletech Allsphere ODS-2 5 μ). We used a 1 ml min^{-1} flow rate, column temperature of 30°C, and 3-solvent gradient system (Jeffrey et al., 1997). The pigments were identified by retention time and absorption spectrum, and their concentrations analyzed by Dionex Chromeleon software. The HPLC was calibrated with pigment standards obtained from the International Agency for ^{14}C Determination (DHI Water and Environment), Hørsholm, Denmark.

Sample preservation, microscopic counts, and estimation of biomass from counts

HPLC can only reliably classify phytoplankton communities to the lowest commonality level of the pigments analyzed, in this case to division level (Havens et al., 1999), while microscopy can detect changes in composition at the level of genus or species (Roy et al., 1996). For more detailed examination of the phytoplankton communities of stations 1 and 6, we also quantified phytoplankton community composition by microscopy.

Water samples preserved in 1% Lugol's solution were concentrated by gravity sedimentation. Phytoplankton counts were made with an Olympus IMT-2 inverted microscope at 600× magnification on random non-overlapping fields until at least 100 units of the most abundant species larger than about 2 μm (nanoplankton) in diameter were counted (APHA, 1995). Based on a Poisson distribution, for 100 units counted and 95% confidence interval, the counting error is ±20% (APHA, 1995).

Identification of nanoplankton was made at the genus level.

The average biovolume of each identified phytoplankton genus was calculated from its geometrical shape (Wetzel & Likens, 2000) and average dimensions. Genus-specific biomass was calculated using the equations of Menden-Deuer & Lessard (2000):

$$\text{For diatoms :} \quad \log \text{pgC l}^{-1} = -0.541 + \left[0.811 * \log\left(\text{cell } \mu\text{m}^{-3}\text{l}^{-1}\right)\right]$$

$$\text{For other protists :} \quad \log \text{pgC l}^{-1} = -0.665 + \left[0.939 * \log\left(\text{cell } \mu\text{m}^{-3}\text{l}^{-1}\right)\right]$$

Genus-specific biomass per liter was obtained from the product of cell abundance and cell biomass.

Data analysis

Correlation analysis was used to quantify degrees of association between pigment concentrations and the biomass of each phytoplankton group. Factorial analysis of variance (ANOVA) was used to determine the relationships of station and date to environmental (TDN, TDP, turbidity) and biological response variables (productivity, biomass, P:B ratio, and pigment concentrations). For the ANOVA, we combined data by season with four sampling dates in March–May 2004 considered spring, five sampling dates in June–August 2004 considered summer, and four sampling dates in September–November 2004 considered fall. Most of the tests met the assumptions of ANOVA for normality (Kolmogorov-Smirnov Test) and equal variance (Levene's Test). In a few cases, where the data were not normally distributed and/or variance was unequal, we performed ANOVA after $\log_{10}$ transformation of the data. The results for ANOVA reported here are for the untransformed values.

For each significant ANOVA, a Tukey's post hoc test was conducted to determine which station means were significantly different. ANOVA and Tukey's test used the GLM procedure in STATISTICA (StatSoft, Inc.).

Results

Physical and chemical conditions

The deepest location in the Sardis Reservoir was nearest to the dam (station 1) and the shallowest location near the mouth of the river (station 6) (Table 1). The average depth at station 1 varied between 12 m in spring and fall, and 16 m in summer. As indicated by the mixing depths, the reservoir was well mixed in spring and fall, whereas it was stratified at deeper stations in summer. At station 1, during summer the water column was typically mixed to 5-m depth. The average temperature at 0.5 m depth was fairly similar throughout the reservoir in a given season, ranging between 29°C in summer and 20°C in fall.

Hydraulic residence time was mostly <100 days through winter and early spring 2004, increased rapidly starting in April to about 1,200 days in June,

Table 1 Mean values of depth, mixing depth, and temperature at Sardis Reservoir between March and December 2004

At all stations, $n = 4$ in spring (Sp) and fall (Fa) and $n = 5$ in summer (Su); except at station 5, $n = 1$ in spring and fall

Station	Depth (m)			Mixing depth (m)			Temperature (°C)		
	Sp	Su	Fa	Sp	Su	Fa	Sp	Su	Fa
1	12	16	12	10	5	11	20	28	23
2	6	6	2	5	4	2	20	28	23
3	7	11	7	6	4	7	22	28	22
4	3	6	3	3	2	3	22	29	24
5	2	3	2	2	2	1	26	28	27
6	4	5	3	4	4	3	23	28	21

started to gradually decrease in July, generally remaining low until the following spring 2005 (Fig. 2a).

At all stations, turbidity increased during fall, remained high in spring, and steadily decreased in summer (Fig. 2b). There was a spatial gradient in turbidity which increased from the stations near the dam (stations 1–3) to the stations near the main river inflow (stations 4–6), with station 6 having the highest and station 1 the lowest turbidity from May to at least November (Table 2). In spring, turbidity conditions were similar at all stations.

TDN and TDP values in summer showed a slight gradient from river to dam. TDN and TDP varied seasonally with high spring values and generally lower summer and fall values (Table 2). Winter values of soluble nitrate-nitrogen (NO_3-N) and phosphate-phosphorus (PO_4-P) were reported to be higher by Ochs & Rhew (1997).

Phytoplankton biomass and production

Light-saturated (400 µmol PAR m^{-2} s^{-1}) phytoplankton production occurred to a depth of 1.4 m at station 1 and 1 m at station 6 during summer (Fig. 2c). At station 1, the depth of the saturating light level mirrored inversely the changes in turbidity, with an increase from spring to summer and a gradual decline through fall. At station 6, however, there was no apparent trend in the depth of light-saturated photosynthesis between March and November 2004.

Phytoplankton biomass in the reservoir, estimated as Chl *a*, exhibited transient peak concentrations in spring and summer, but generally increased from early spring to fall (Fig. 3a). In 2004, Chl *a* biomass ranged between 3 and 4 mg m^{-3} in spring and 13–19 mg m^{-3} in fall (Fig. 3a). In 2005, Chl *a* biomass was about 10 mg m^{-3} in March, decreasing to <5 mg m^{-3} in April (Fig. 3a). Based on our results for 2005, and the study of Ochs & Rhew (1997), it is suspected that a transient spring peak in phytoplankton biomass occurred shortly before we first sampled in 2004.

There was a spatial gradient in phytoplankton biomass which increased from stations near the dam toward stations closer to the Little Tallahatchie River (Fig. 3a; Table 2). At all stations, spatial variation in biomass was most pronounced in summer, while station 1 and station 6 were significantly different from each other in all three seasons (Table 2). Among the three embayment areas, station 4 (at the Toby Tubby Creek tributary) had the highest seasonal mean biomass in all three seasons.

In 2004, light saturated phytoplankton production decreased from about 50 mg C m^{-3} h^{-1} in spring to <10 mg C m^{-3} h^{-1} in mid-summer and gradually increased up to 100 mg C m^{-3} h^{-1} in fall (Fig. 3b). In spring 2005, production returned to spring values of the previous year. Stations near the river had higher seasonal mean production values than stations near the dam, although the differences were not always statistically significant (Table 2). At all stations, the P:B ratio was highest in spring, least during summer, and slowly increased during fall (Fig. 3c). In contrast to the spatial pattern in production, during summer stratification, the lowest P:B values were at the more turbid, but phytoplankton-rich, riverine stations (Table 2).

Phytoplankton community composition by HPLC pigment analysis

Chl *b*, a diagnostic pigment for chlorophytes, exhibited summer peaks in concentration at stations 4, 5,

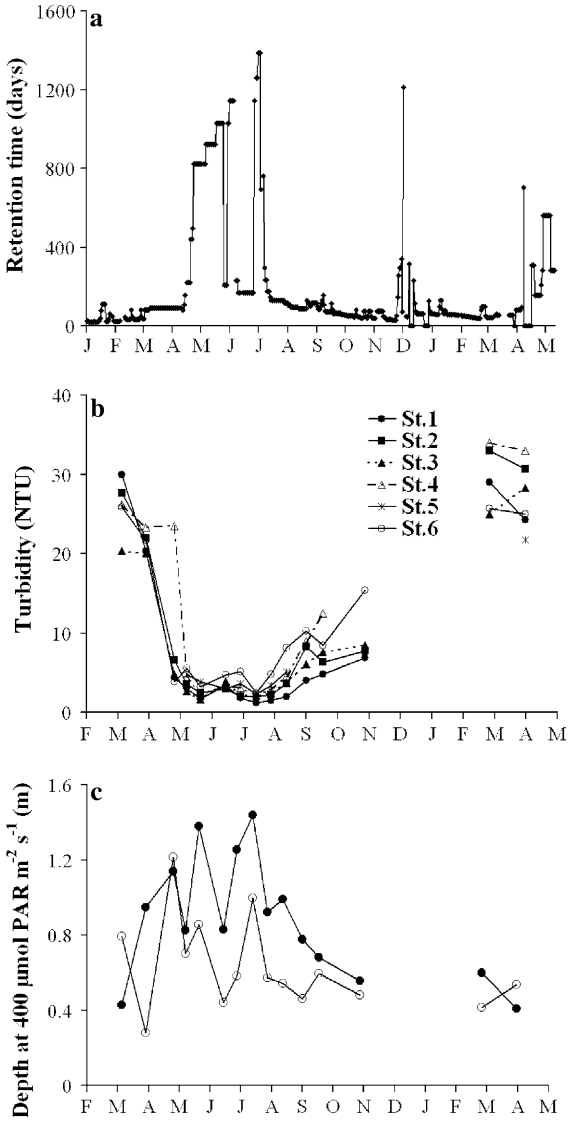

Fig. 2 Physical and chemical characteristics of water by station and month for 2004 and spring 2005. (**a**) Hydraulic residence time; (**b**) Turbidity; (**c**) Depth of saturating light level (400 µmol PAR m^{-2} s^{-1}) at down-lake (Station 1) and up-lake (Station 6) regions

and 6, whereas a fall peak was observed at stations 1, 2, and 3 in 2004 (Fig. 4a). The three stations near the dam (stations 1–3) had lower seasonal means of Chl *b* than the three stations near the river (stations 4–6; see Table 2). Differences in Chl *b* concentration between stations 1 and 6 were statistically significant in all three seasons.

Fucoxanthin, a diagnostic pigment for diatoms, declined in concentration from spring to summer, and then increased several-fold in fall 2004. The difference between stations 1 and 6 was statistically significant in all three seasons, with station 6 having the higher seasonal mean values (Table 2).

Zeaxanthin, a diagnostic pigment for cyanobacteria, increased in concentration from spring to summer and decreased in late-fall at all stations in 2004, and concentrations were low in spring 2005 (Fig. 4c). Stations 1 and 6 were significantly different from each other in all three seasons; with station 6 having higher seasonal mean values (Table 2).

Peridinin was rarely detectable by HPLC. Two genera of dinoflagellates, *Ceratium* sp. and *Peridinium* sp., although never sufficiently abundant to be detected by peridinin, were detected by microscopy in summer. Although cryptophytes occurred throughout the year, alloxanthin, a signature pigment of cryptophytes, was not reliably identified by HPLC.

Relative phytoplankton community composition, as indicated by the ratio of signature pigments to Chl *a*, was different between stations 1 (deeper, less turbid) and 6 (shallow, more turbid) during summer, 2004 (Fig. 5). The Chl *b*:Chl *a* ratio was higher at station 6 than at station 1 (Fig. 5a). The fucoxanthin:Chl *a* ratio, with the exception of one date, was consistently higher at station 6 than at station 1 (Fig 5b). In contrast, except for a transient peak in the cyanobacterial proportion of phytoplankton at station 6 in late spring, from May to late August the zeaxanthin:Chl *a* ratio was higher at station 1 (Fig. 5c).

Phytoplankton biomass by microscopy and correlation with pigments

Population dynamics of the major phytoplankton groups, as determined by microscopy, mostly followed the pattern indicated by pigment concentrations (Fig. 6). Chlorophyte biomass peaked briefly in summer, decreased at the end of summer, and increased again in fall (Fig. 6a). Diatom biomass which was high in spring declined to minimum values in summer and exhibited peaks in fall at both stations (Fig. 6b). Cyanobacterial biomass was high in summer, decreased slightly at the end of summer, and slightly increased in fall (Fig. 6c). During the stratified summer period, there was a greater biomass of chlorophytes and diatoms at station 6 than at station 1

Table 2 Two-way ANOVA for study parameters for the year 2004

Variables	Season	Date		Station		Station means					
		P	df	*P*	df	1	2	3	4	5	6
Turbidity (NTU)	Spring	0.0001	3	0.0001	4	14.43^{a}	14.95^{a}	11.97^{a}	19.36^{b}	–	12.16^{a}
	Summer	0.001	4	0.0001	5	1.87^{a}	2.34^{b}	2.45^{b}	2.73^{c}	3.25^{d}	4.08^{e}
	Fall	0.0001	3	0.0001	4	4.44^{a}	6.48^{b}	6.46^{b}	9.62^{c}	–	10.56^{c}
TDN (mg l^{-1})	Spring	0.005	3	NS	4	0.49^{a}	0.5^{a}	0.58^{a}	0.49^{a}	–	0.52^{a}
	Summer	0.01	4	NS	5	$0.24^{a,b,c}$	$0.25^{a,b,c}$	$0.31^{a,b,c}$	0.23^{b}	$0.25^{a,b,c}$	0.34^{c}
	Fall	0.0001	3	0.0001	4	0.26^{a}	$0.24^{a,b}$	0.27^{a}	0.19^{b}	–	0.26^{a}
TDP (mg l^{-1})	Spring	0.04	3	NS	4	0.05^{a}	0.06^{a}	0.05^{a}	0.05^{a}	–	0.05^{a}
	Summer	0.0001	4	NS	5	0.017^{a}	0.02^{a}	0.04^{a}	0.014^{a}	0.014^{a}	0.019^{a}
	Fall	0.0001	3	NS	4	0.025^{a}	0.03^{a}	0.023^{a}	0.018^{a}	–	0.027^{a}
Biomass (mg Chl *a* m^{-3})	Spring	0.0001	3	0.0001	4	2.41^{a}	2.87^{a}	$2.99^{a,b}$	4.01^{b}	–	6.52^{c}
	Summer	0.0001	4	0.0001	5	5.12^{a}	$6.31^{a,b,d}$	$7.76^{b,c,d}$	$9.45^{c,d,e}$	8.27^{d}	10.73^{e}
	Fall	0.0001	3	0.0001	4	11.35^{a}	11.25^{a}	9.38^{b}	$12.28^{a,c}$	–	13.76^{c}
Production (mg C m^{-3} h^{-1})	Spring	–	–	0.023	4	43.00^{a}	41.75^{a}	48.60^{a}	36.71^{a}	–	69.59^{a}
	Summer	0.0001	3	0.0001	5	12.19^{a}	11.74^{a}	13.7^{a}	13.48^{a}	14.89^{a}	18.44^{b}
	Fall	0.0001	3	0.0001	4	52.13^{a}	42.28^{b}	52.37^{a}	45.08^{b}	–	65.8^{c}
P:B (mg C mg Chl a^{-1} h^{-1})	Spring	–	–	0.05	4	14.87^{a}	9.07^{a}	11.57^{a}	7.30^{a}	–	7.73^{a}
	Summer	0.001	3	0.02	5	2.52^{a}	$1.87^{a,b}$	1.71^{b}	1.27^{b}	1.61^{b}	1.47^{b}
	Fall	0.0001	3	0.0001	4	$4.42^{a,c}$	3.74^{c}	5.72^{b}	$4.83^{a,b,c}$	–	$4.93^{a,b}$
Chl *b* (mg m^{-3})	Spring	0.0001	3	0.003	4	0.03^{a}	$0.12^{a,b}$	0.15^{b}	0.21^{b}	–	0.21^{b}
	Summer	0.0001	4	0.0001	5	0.18^{a}	0.31^{a}	0.26^{a}	0.67^{b}	0.62^{b}	0.76^{b}
	Fall	0.001	3	0.0001	4	0.38^{a}	0.56^{b}	0.31^{a}	0.63^{b}	–	0.62^{b}
Fucoxanthin (mg m^{-3})	Spring	0.006	3	0.0001	4	1.46^{a}	1.55^{a}	1.514^{a}	1.86^{b}	–	2.06^{b}
	Summer	NS	4	0.0001	5	0.55^{a}	0.46^{a}	0.64^{a}	0.69^{a}	0.8^{a}	1.4^{b}
	Fall	0.0001	3	0.0001	4	2.67^{a}	2.52^{a}	2.59^{a}	2.78^{a}	–	3.78^{b}
Zeaxanthin (mg m^{-3})	Spring	NS	3	NS	4	0.27^{a}	$0.37^{a,b}$	0.41^{b}	$0.47^{b,c}$	–	0.58^{c}
	Summer	0.0001	4	0.003	5	1.41^{a}	$1.91^{a,b}$	$1.64^{a,b}$	2.54^{b}	2.33^{b}	2.11^{b}
	Fall	0.011	3	0.006	4	1.47^{a}	3.57^{b}	1.54^{a}	3.36^{b}	–	2.23^{c}

Two main effects of date and station location were tested for the given variables. Station means having the same subscript are not significantly different from each other at $P < 0.05$. NS = not significant. Cells lacking values indicate no measurements

(Fig. 6a, b), whereas cyanobacterial biomass reached its maximum value at station 1 (Fig. 6c). Cryptophytes occurred throughout the year and were more abundant in spring and fall at station 1 (Fig. 6d). Euglenoids were less abundant than other phytoplankton; they were more common in fall at both stations.

Similar phytoplankton genera were found at station 1 and station 6. Species of *Ankistrodesmus*, *Scenedesmus*, *Selenastrum*, *Staurastrum*, *Tetraedron*, and *Crucigenia*, were the most abundant chlorophytes. Species of *Cyclotella*, *Aulacoseira*, *Asterionella*, *Nitzschia*, and *Synedra* were the dominant diatoms. Species of *Pseudanabaena*, *Anabaena*, and *Raphidiopsis* were the most abundant filamentous cyanobacteria. Species of *Cyclotella, Asterionella*, *Nitzschia*, and *Ankistrodesmus*, were among the first colonizers in the early spring, closely followed by *Aulacoseira*. By the mid-spring when diatoms started to decline, cryptophytes increased in abundance. Filamentous cyanobacteria were most abundant during summer throughout the reservoir. One species of *Raphidiopsis*, most likely *R. curvata*, occurred briefly, only during late summer and early fall. The secondary bloom of diatoms in fall consisted of all the major species. Species of *Synedra*, *Crucigenia*, *Selenastrum*, *Scenedesmus*, and *Merismopedia* were present

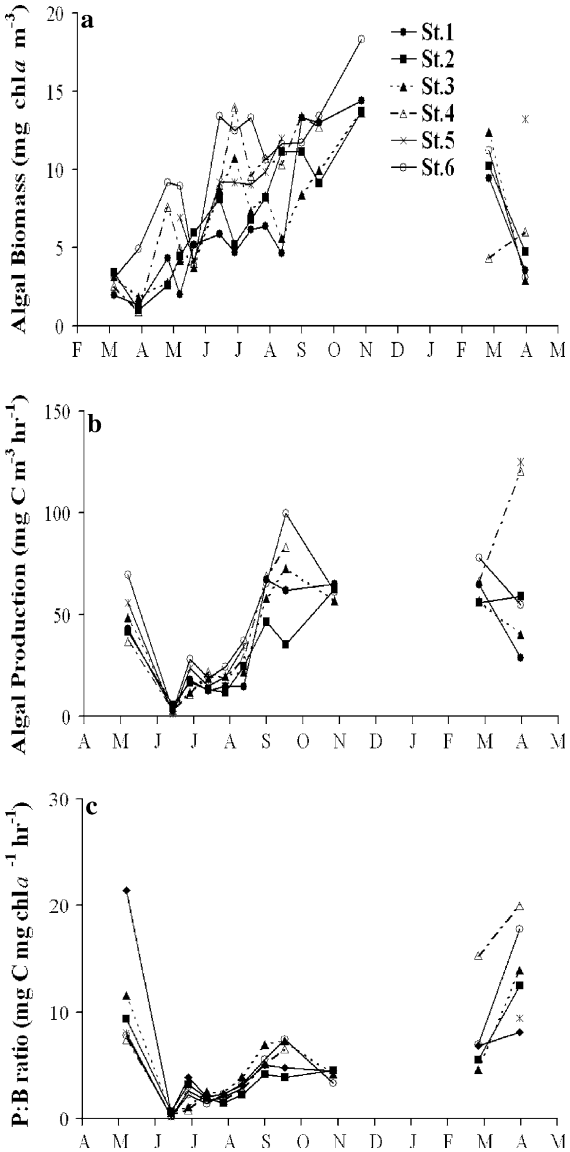

Fig. 3 (**a**) Phytoplankton biomass; (**b**) Phytoplankton production; (**c**) Production to biomass ratio. The results are by station and month in 2004 and spring 2005

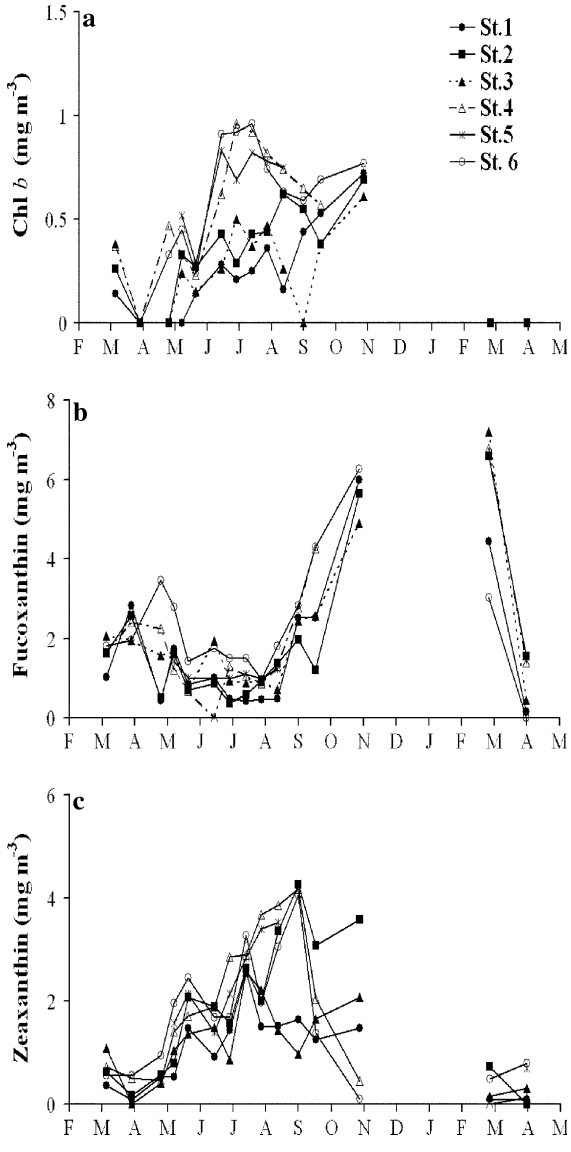

Fig. 4 Pigment concentrations by station and month in 2004 and spring 2005. (**a**) Chl *b*; (**b**) Fucoxanthin; (**c**) Zeaxanthin. Zero values have been assigned where pigments were not detected by HPLC

through out the sampling period, while *Staurastrum* and *Tetraedron* appeared only in late spring. This transition in species was more pronounced at station 1 (down-lake) compared to station 6 (up-lake) of the reservoir.

The two methods of estimating the presence of particular phytoplankton groups, by pigment concentration and from microscopic counts and biovolume estimates, were positively correlated for all phytoplankton groups: chlorophytes and Chl *b* ($r = 0.40$), diatoms and fucoxanthin ($r = 0.43$), and cyanobacteria and zeaxanthin ($r = 0.38$). The correlations of zeaxanthin with chlorophyte biomass and Chl *b* with euglenoid biomass were not significant (Table 3).

Discussion

Sardis Reservoir undergoes dramatic changes in HRT from water retention and draw down in response to

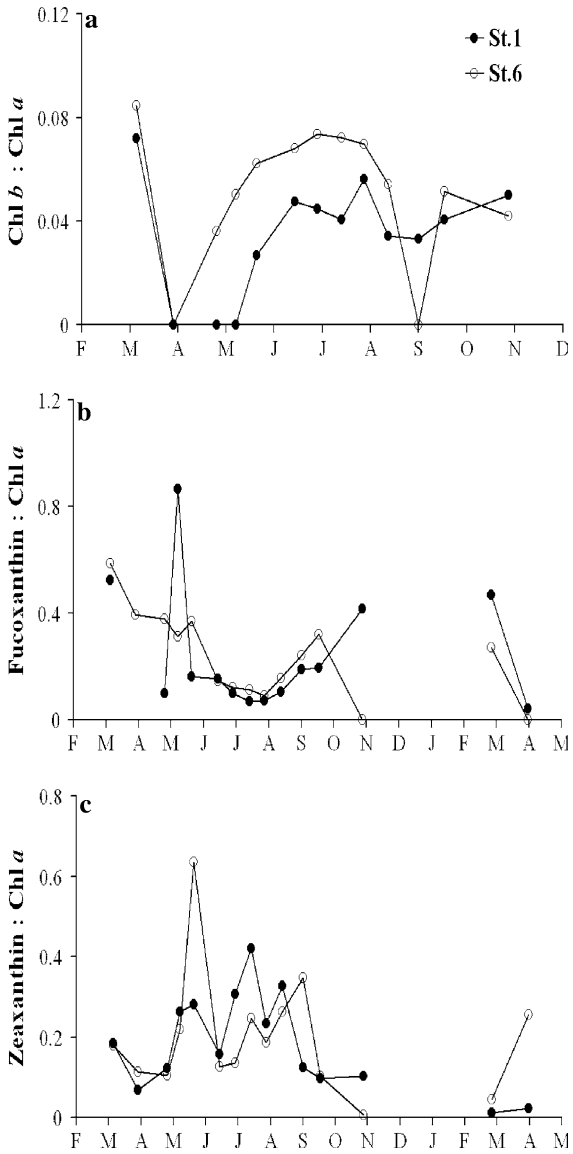

Fig. 5 Pigment ratios by month at down-lake (Station 1) and up-lake (Station 6) regions in 2004 and spring 2005. (**a**) Chl *b*: Chl *a*; (**b**) Fucoxanthin: Chl *a*; (**c**) Zeaxanthin: Chl *a*

flood control operations. In the year of this study, reservoir operation altered HRT by an order of magnitude, from about 100 days in mid-April to over 1,000 days later in the same month. Between late-fall and mid-spring, when HRT is short, longitudinal gradients in physical, chemical, and plankton community variables are not evident (Ochs & Rhew, 1997). However, as the reservoir fills, HRT increases, the water column stratifies, and physical and chemical conditions vary, spatial heterogeneity in phytoplankton community characteristics develops. Other reservoir studies have reported similar longitudinal gradients in nutrients (N and P), phytoplankton biomass, and production (Knowlton & Jones, 1995; Schallenberg & Burns, 1997; Buckaveckas & Crain, 2002), including the study of Sardis Reservoir by Ochs & Rhew (1997) when such variation was most pronounced during the summer period of long HRT. In this study, we have shown that at the same time of year, summer, there also is distinct spatial variation in phytoplankton community composition.

Despite reservoir operation impacts on hydrology, the seasonal succession from spring to summer of the phytoplankton community in Sardis Reservoir resembled the pattern described for a model monomictic mesotrophic temperate lake (Sommer et al., 1986; Wetzel, 2001). With spring circulation there was a rapid increase in fast-growing diatoms and chlorophytes. During this period of spring mixing and warming when nitrogen and phosphorus were most probably available, algal production was relatively high, and the P:B ratio was at a maximum for the year. As thermal stratification developed, diatoms declined, and more slow-growing, warm-temperature tolerant, heterocystous cyanobacteria and chlorophytes became increasingly important. Corresponding to a decline in nitrogen and phosphorus levels, algal production and the P:B ratio declined. Although algal biomass and production, slightly, increased during summer, the P:B ratio remained low compared to spring values, suggesting nutrient limitation. As the reservoir switched from having a stratified water column in late summer to that of a well-mixed fast-flowing system in the fall, the phytoplankton community was rapidly altered, with a major secondary bloom of diatoms and chlorophytes. The fall bloom was mirrored by an increase in algal production, and a modest increase in the P:B ratio, indicating some release from nutrient limitation of the phytoplankton community.

Interestingly, the typical pattern in phytoplankton seasonal succession, as described for mesotrophic temperate lakes (Wetzel, 2001), was mimicked in the reservoir as spatial variation in summer. Throughout summer, the up-lake region (station 6) of the reservoir was more turbulent, turbid, and in greater contact with the sediments (and thereby more nutrient rich), as compared with the more clear, stratified, and

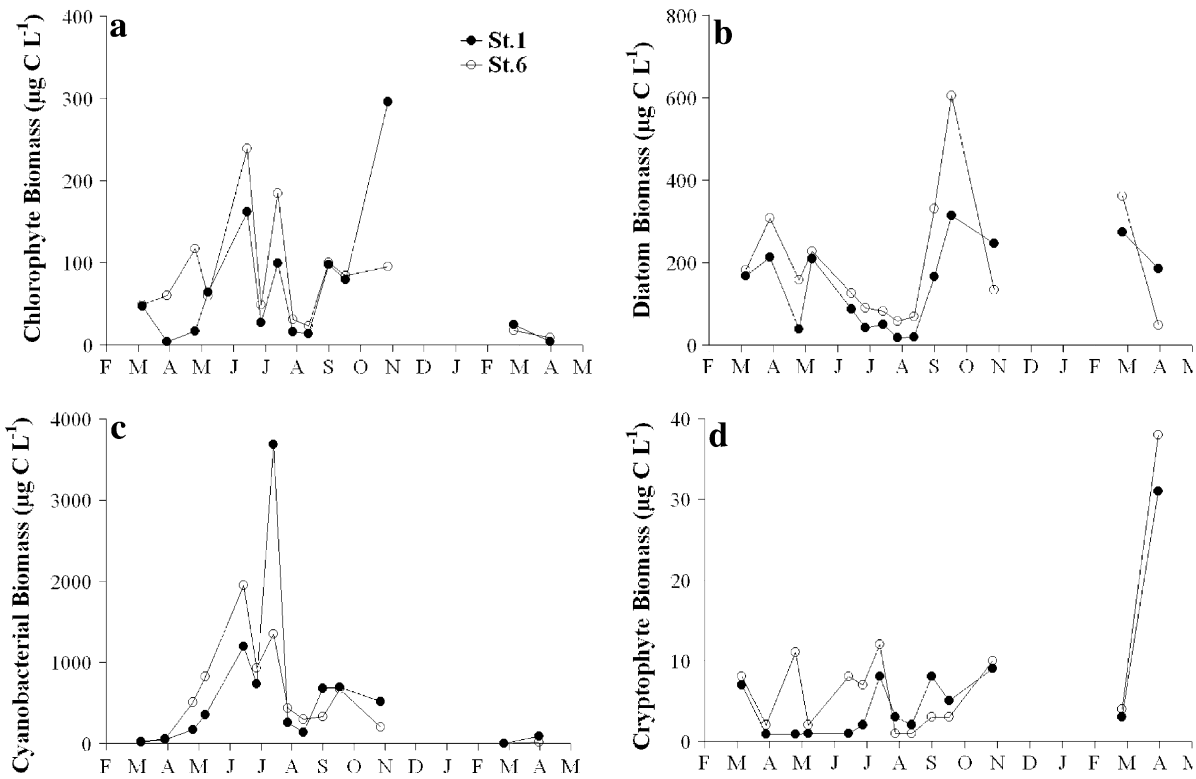

Fig. 6 Biomass of phytoplankton groups by month down-lake (Station 1) and up-lake (Station 6) in 2004 and spring 2005 estimated from the microscope counts. In 2004, there were two sampling dates in each of month May, July, August, and September. (**a**) Chlorophytes; (**b**) Diatoms; (**c**) Cyanobacteria; (**d**) Cryptophytes

Table 3 Pearson correlation coefficients (*r*-values) for algal biomass (as carbon equivalents) and algal pigments

Biomass	Pigment		
	Chl-*b* (mg m^{-3})	Fucoxanthin (mg m^{-3})	Zeaxanthin (mg m^{-3})
Chlorophytes (µg C l^{-1})	0.40*	0.19	0.16
Diatoms (µg C l^{-1})	0.04	0.43*	−0.14
Cyanobacteria (µg C l^{-1})	0.36*	−0.18	0.38*
Euglenoid (µg C l^{-1})	0.15	0.28	−0.16

Significance ($P < 0.01$) is indicated by an asterisk ($n = 56$)

nutrient-impoverished down-lake region (station 1). In these respects, the up-lake and down-lake regions resembled typical temperate lake spring and summer conditions, respectively. Corresponding to these spatial differences in physicochemical conditions, the phytoplankton communities from these two regions mimicked spring and summer communities. At the up-lake region (station 6), even in mid-summer, there was a relatively spring-like flora with chlorophytes and diatoms being a larger proportion of phytoplankton biomass. Within the down-lake region (station 1), in contrast, a more typical mid-summer lake flora developed, with heterocyst-bearing cyanobacteria a larger proportion of phytoplankton biomass on most sampling dates. Habitat differences spatially (e.g., riverine versus lacustrine) can promote simultaneous growth of different communities of phytoplankton within one ecosystem as the environmental conditions favor specific species. Habitat differences might also promote spatial variation in physiological condition (e.g., concentrations of pigments or storage compounds) of a particular phytoplankton community. This aspect of the phytoplankton ecology of spatially heterogeneous systems would benefit from further study.

Following Reynolds trait-separated functional grouping of phytoplankton (Reynolds, 1997; Reynolds et al., 2002), there was a lakewide succession that follows the pattern of codons B/C/D → Y → S1/H1 → S2, beginning in spring and progressing toward summer. The spring flora consisted largely of rapidly growing diatoms, corresponding to codons B (*Cyclotella*, *Aulacoseira*), C (*Aulacoseira, Asterionella*), and D (*Nitzschia*), that are favored under the physical conditions of high turbidity and relatively available TDN and TDP. These conditions, which also occur in the reservoir after the fall overturn, are more pronounced and longer lasting at the riverine end of the reservoir. The diatom community observed in spring in Sardis Reservoir is characteristic of vernal blooms in mesotrophic to eutrophic waters. Small centric single-cell diatoms like *Cyclotella* that first dominated the community were replaced later in spring by large colonial centric diatoms like *Aulacoseira*. In the transition from spring to summer, there was a decline in diatoms concomitant with decreasing TDN and TDP concentrations, probable Si exhaustion, and development of an increasingly stable water column, especially at the lower, more lacustrine portion of the reservoir. With the decrease in diatoms, cryptophytes under codon Y increased in abundance. Chlorophytes, especially pertaining to codon J, were present throughout the sampling period though their biomass was higher in mid-summer and late-fall. As nutrient limitation progressed, there was a pronounced increase in the proportion of filamentous cyanobacteria, corresponding to codons S1 (e.g., *Pseudanabaena*) and H1 (e.g., *Anabaena*), that are characterized by their capacity for buoyancy control and nitrogen fixation. As riverine flow was reestablished in late summer, turbidity increased across the reservoir and cyanobacteria of codon S2 (e.g., *Raphidiopsis*) briefly become prevalent, especially at the deeper station 1. By mid-fall, stratification had broken, nutrient concentrations had increased, and retention time was at a minimum resulting in a secondary bloom of diatoms, represented by codons B/C/D, and cryptophytes.

In addition to nutrient effects on phytoplankton composition and biomass, there is the potential effect of spatially differential zooplankton grazing. Here, we can only speculate as we have no data on spatial variation within the reservoir of zooplankton abundance or composition. Perhaps due to a higher flow rate, and greater turbidity, zooplankton are less abundant, or less important as grazers, in the upper, more riverine end of the reservoir (c.f. Pace et al., 1992). If so, this would allow small edible, higher nutritional-quality algae such as diatoms and chlorophytes to survive longer at one end of the reservoir than the other. In contrast, a greater impact of zooplankton grazing at the lower, more lacustrine end of the reservoir would favor less edible and less nutritious algae such as cyanobacteria**.** If so, in addition to the observed chemical, physical, and biological gradients along the axis of the reservoir, there also is a gradient in the relative importance of bottom-up nutrient control versus top-down grazer control of phytoplankton biomass and community composition.

Spatial variation in physicochemical conditions and phytoplankton community structure in Sardis Reservoir may also be influenced by variation in land-use in the LTW or sub-watersheds draining the three major tributaries. The embayment areas (stations 2, 4, and 5) are affected by inputs from the Little Tallahatchie River, inputs from tributary creeks draining sub-watersheds, and interactions with the reservoir. Although results were not always statistically significant, it is interesting that among the embayment areas, station 4 (Toby Tubby Creek) generally had higher mean phytoplankton biomass than station 2 (Clear Creek) and station 5 (Hurricane Creek). The higher phytoplankton biomass at the Toby Tubby Creek embayment compared to the Clear Creek embayment might be due to its shallow depth which facilitates nutrient regeneration from the sediments, and greater average light availability (Rhew & Ochs, 2000). In addition, because the Toby Tubby sub-watershed has a higher percentage of urban and residential land-use than the other two sub-watersheds, relatively more nutrients could be entering the reservoir from Toby Tubby Creek. Currently, however, we do not have information on the chemical properties of streams draining these sub-watersheds.

In this study, we have documented that along with variation in phytoplankton biomass and productivity, there is a distinct spatial variation in phytoplankton community composition along the longitudinal axis of a large southeastern U.S. reservoir during the summer period of long HRT. A model of phytoplankton succession in a typical temperate lake (Wetzel, 2001) applies well to this system between

spring and fall with modification needed for the influence of transient but predictable longitudinal spatial gradients in physicochemical conditions, which clearly affects the phytoplankton community development. Understanding of the causal mechanisms for temporal and spatial variation in reservoir phytoplankton community characteristics is essential for resource managers concerned with fisheries, eutrophication, aesthetics, or drinking water quality.

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References

APHA (American Public Health Association), 1995. Standard Methods for the Examination of Water and Wastewater. APHA, Washington, D.C.

Aumen, N. G., C. L. Christ, D. E. Miller & K. O. Meals, 1992. Particulate organic carbon supply and trophic dynamics in a Mississippi flood-control reservoir dominated by gizzard shad (*Dorosoma cepedianum*). Canadian Journal of Fisheries and Aquatic Sciences 49: 1722–1733.

Bailey-Watts, A. E., L. Kirika, L. May & D. H. Jones, 1990. Changes in phytoplankton over various time scales in a shallow, eutrophic loch: The Loch Leven experience with special reference to the influence of flushing rates. Freshwater Biology 23: 85–111.

Bettoli, P. W., M. F. Cichra & W. J. Clark, 1985. Phytoplankton community structure and dynamics in Lake Conroe, Texas. Texas Journal of Science 36: 221–233.

Bukaveckas, P. A. & A. S. Crain, 2002. Inter-annual, seasonal and spatial variability in nutrient limitation of phytoplankton production in river impoundment. Hydrobiologia 481: 19–31.

Charles, J. P. & J. R. Kryskalla, 2003. Methods of analysis by the U.S. geological survery national water quality laboratory—evaluation of alkaline persulphate digestion as an alternative to kjeldahl digestion for determination of total and dissolved nitrogen and phosphorus in water. Water Resources Investigation Report 03-4174. U.S. Geological Survey, Denver, Colorado.

Ford, D. E., 1990. Reservoir Transport Processes. In Thornton, K. W., F. E. Payne & B. L. Kimmel (eds), Reservoir Limnology: Ecological Perspectives. Wiley-Interscience Publication, New York, 15–41.

Havens, K. E., A. D. Steinman, H. J. Carrick, J. W. Louda, N. M. Winfree & E. W. Baker, 1999. Comparision analysis of lake periphyton communities using high performance liquid chromatography (HPLC) and light microscope counts. Aquatic Sciences–Research Across Boundaries 61: 307–322.

Jeffrey, S. W., R. E. C. Mantoura & S. W. Wright, 1997. Phytoplankton Pigments in Oceanography: Guidelines to Modern Methods. UNESCO, Paris.

Kalff, J., 2002. Limnology. Prentice Hall, New Jersey.

Kimmel, B. L., T. L. Owen & L. J. Paulson, 1990. Reservoir Primary Production. In Thornton, K. W., F. E. Payne & B. L. Kimmel (eds), Reservoir Limnology: Ecological Perspectives. Wiley-Interscience Publication, New York: 133–174.

Knowlton, M. F. & J. R. Jones, 1995. Temporal and spatial dynamics of suspended sediment, nutrients, and algal biomass in Mark Twain Lake, Missouri. Archiv für Hydrobiologie 135: 145–178.

McCullough, J. D., 1978. A study of phytoplankton primary productivity and nutrient concentrations in Livingston Reservoir, Texas. Texas Journal of Science 30: 77–387.

Menden-Deuer, S. & E. J. Lessard, 2000. Carbon to volume relationships for dinoflagellates, diatoms, and other protist plankton. Limnology and Oceanography 45: 569–570.

MARIS (Mississippi Automated Resource Information System), 2005. MARIS home page <http://www.maris.state.ms.us> Accessed 2005 May 1.

Ochs, C. A. & K. Rhew, 1997. Population dynamics of autotrophic picoplankton in a southeastern U.S. Reservoir Internationale Revue gesamten Hydrobiologie 82: 293–313.

Nogueira, M. G., 2000. Phytoplankton composition, dominance and abundance as indicators of environmental compartmentalization in Jurumirim Reservoir (Paranapanema River), São Paulo, Brazil. Hydrobiologia 431: 115–128.

Pace, M. L., S. E. G. Findlay & D. Lints, 1992. Zooplankton in advective environments: The Hudson River community and a comparative analysis. Canadian Journal of Fisheries and Aquatic Sciences 49: 1060–1069.

Pearl, H. W., M. L. Valdes, J. L. Pinckney, M. F. Piehler, J. Dyble & P. H. Moisander, 2003. Phytoplankton photopigments as indicators of estuarine and coastal eutrophication. Bioscience 53: 953–964.

Pickney, J. L., T. L. Richardson, D. F. Millie & H. W. Pearl, 2001. Application of photopigment biomarkers for quantifying microalgal community composition and *in situ* growth rates. Organic Geochemistry 32: 585–595.

Ramberg, L., 1987. Phytoplankton succession in the Sanyati basin, Lake Kariba. Hydrobiologia 153: 193–202.

Reynolds, C. S., 1997. Vegetation Processes in the Pelagic. A Model for Ecosystem Theory. ECI, Oldendorf, 7–16.

Reynolds, C. S., V. Huszar, K. Kruk, L. Naselli-Flores & S. Melo, 2002. Towards a functional classification of the freshwater phytoplankton. Journal of Plankton Research 24: 417–428.

Rhew, K. & C. A. Ochs, 2000. Spatial patterns in autotrophic picoplankton abundance in a reservoir examined using

microcosm experiments. International Revue of Hydrobiology 85: 395–412.
Roy, S., J. P. Chanut, M. Gosselin & T. Sime-Ngando, 1996. Characterization of phytoplankton communities in the lower St. Lawrence estuary using HPLC-detected pigments and cell microscopy. Marine Ecological Progress Series 142: 55–73.
Schallenberg, M. & C. W. Burns, 1997. Phytoplankton biomass and productivity in two oligotrophic lakes of short hydraulic residence time. New Zealand Journal of Marine and Freshwater Research 31: 119–134.
Schlüter, L., T. L. Lauridsen, G. Krogh & T. Jørgensen, 2006. Identification and quantification of phytoplankton groups in lakes using new pigment ratios – a comparison between pigment analysis by HPLC and microscopy. Freshwater Biology 51: 1474–1485.
Soballe, D. M. & D. M. Kimmel, 1987. A large-scale comparison of factors influencing phytoplankton abundance in rivers, lakes, and impoundments. Ecology 68: 1943–1954.
Sommer, U., Z. M. Gliwicz, W. Lampert & A. Duncan, 1986. The PEG-model of seasonal succession of planktonic events in fresh waters. Archiv für Hydrobiologie 106: 433–471.
USDA-NRCS (United States Department of Agriculture – Natural Resources Conservation Service), 2005. USDA-NRCS home page <http://www.nrcs.usda.gov> Accessed 2007 Jan 12.
USACE (United States Corps of Engineers), 2005. USACE home page <http://www.rivergages.com> Accessed 2005 May 10.
Wetzel, R. G., 2001. Limnology: Lake and River Ecosystems. Academic Press, New York, 350.
Wetzel, R. G. & G. E. Likens, 2000. Limnological Analysis. Springer-Verlag, New York, 219.
Zohary, T., A. M. Pais-Madeira, R. Robarts & K. D. Hambright, 1996. Interannual phytoplankton dynamics of a hypertrophic African lake. Archiv für Hydrobiologie 136: 105–126.